



ADVANCES IN THE ECOLOGY OF LAKE KARIBA

Edited by Jacques MOREAU



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Cover Top: Typical ringnets as utilized in Kapenta fisheries on Lake Kariba
Bottom: Lake Kariba: The littoral area and draw-down zone
Back cover: Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

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BIOMASS, ECOLOGY AND PRODUCTION OF BENTHIC FAUNA IN LAKE KARIBA

Nils Kautsky and Martina Kiibus

INTRODUCTION

Studies on benthic invertebrates of African freshwater ecosystems are still in their infancy, although the benthic fauna is ecologically important in the food chain as a link between heterotrophic and autotrophic microfloral production, and the production of economically important higher trophic levels such as fish. Invertebrates, both filter feeders and detritus feeders, are also very important in the remineralization of nutrients (Kuenzler 1961, Kautsky and Evans 1987, Kautsky and Wallentinus 1980, Okedi 1990).

African freshwater invertebrates also include a large number of vector species which transmit human diseases such as malaria and schistosomiasis. It is thus important that factors controlling the distribution of such vector species, e.g. schistosomiasis carrying snails should be determined.

In Lake Kariba, explosive development of the invertebrate fauna occurred during the filling phase between 1959 and late 1963, but also after that there have been periods of rapid colonization of invading species (Begg 1970, Balon and Coche 1974, Kenmuir 1980a, Machena 1989 and this volume). The following development was characterized by shoreline development, appearance and expansion of rooted hydrophytes, accumulation of sediments, annual water level fluctuations, and reduced nutrient concentrations (Coche 1974, Balon and Coche 1974, Ramberg *et al.* 1987), which all influenced the development of benthic communities (Machena 1989 and this volume).

Under these changing conditions, McLachlan (1969, 1970) and McLachlan and McLachlan (1971) conducted their detailed studies on benthic invertebrates, particularly on the chironomidae (Diptera) which then dominated the benthos. Benthos surveys conducted in 1969-70 in the Zambian cleared areas of Lake Kariba (Coche 1974) showed how relatively low the abundance of the benthic community still was in areas devoid of submerged vegetation. In 1970, 11 species of molluscs were identified from the Sanyati sub-basin, comprising 2 lamellibranchs and 9 gastropods that had by then colonized the lake (McLachlan 1974).

Up to the end of the 1960's, chironomids and snails dominated the benthos (McLachlan 1969). Bivalves were first noted after 1964 (McLachlan 1967), six years after closure of the dam, and by 1975 mussel beds were well established (Kenmuir 1980a). The first species to appear were *Aspatharia wahlbergi* and *Corbicula africana*, while *Caelatura mossambicensis* and *Mytilus dubia* seem to have colonized later (Kenmuir 1980a). Since the mussels in Lake Kariba

represent a potential resource of proteins that might be exploited, their distribution and biology in the lake was extensively studied by Kenmuir (1980a,b, 1981). Most of the studies on other benthic invertebrates (McLachlan 1967, 1969, 1970, McLachlan and McLachlan 1971) were carried out before the mussel beds established, and only little information is available from the period after the increase in mussels and benthic vegetation during the 1970's.

Before the late 1960's, the establishment of benthic communities seems to have been limited by the rapid rise in water level during the filling phase and the extensive growth of *Salvinia molesta* which formed thick mats on the water surface and occluded light to the bottom. Periods of low oxygen and H_2S formation were also common during that period.

The species diversity of invertebrates in young Lake Kariba is naturally considerably lower than in the evolutionary old African lakes (e.g. Lakes Malawi, Tanganyika and Victoria), although it appears that new species are continuously colonizing the lake.

The main aim of the present study was to determine the factors that control the distribution of benthic communities, to collect the data needed to work out the productivity of the littoral zone and to evaluate its role in the functioning and dynamics of Lake Kariba. In this chapter, the biomass, the vertical and horizontal distribution, and the ecology and production of the benthic invertebrate fauna will be described some 30 years after closure of the dam. Most of the information is based on a diving survey which was carried out in 1984 (Machena and Kautsky 1988) and some follow up studies (Machena 1989, Machena *et al.* 1990, Ramberg *et al.* 1987), but the literature will also be reviewed and the data compared with other lakes in Africa. The ecophysiology and production data are mainly based on a study by Kiibus and Kautsky (1996).

MATERIAL AND METHODS

A diving survey was carried out along eighteen transects that were spaced to cover all shoreline types along the whole length of the Zimbabwean shore (Figure 6.1, Machena this volume). Some areas near river mouths and fishing villages had to be excluded because of crocodiles and bilharzia. Details on the methods are given in Machena and Kautsky (1988).

Each diving transect extended from the shore to the maximum depth inhabited by macrophytes or mussels. The divers recorded the species composition, abundance and cover of the vegetation and abundance of mussels, the distance from the shore and the depth. Quadrats (0.5 x 0.5 m) were placed at random in a stratified manner along the transects. The vegetation, including epiphytes, surface sediment, mussels and snails, were collected in 1 mm-mesh sample bags for biomass determination. A total of 279 samples along the 18 transects were collected. During the 1984 investigation, the water level was 7 m below the normal 484 m. a. s. l., due to the 1982–1985 drought.

The total standing stock of biomass for the whole lake was the product of the average biomass in each depth interval and the average bottom area for each m between 0 and 15 m ($105.22 \text{ km}^2 \text{ m}^{-1}$) which was calculated from data in Coche (1968).

The production of benthos was calculated by multiplying our biomass values with estimates of production over biomass (P/B) ratios obtained for the

populations under consideration, or similar ones (Winberg *et al.* 1971, Zaika 1973).

Respiration and the excretion of nutrients ($\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$) was assessed for different sizes of freshly collected mussels (*Aspatharia wahlbergi*, *Corbicula africana* and *Caelatura mossambicensis*). The experiments were carried out in 1.5 l aquaria at 25.2°C. For *A. wahlbergi* and *C. africana*, similar experiments were carried out at higher and lower temperatures. The filtration (clearance) rate of *Aspatharia wahlbergi* was measured spectrophotometrically in 1.5 l aquaria. For experimental setup and details on material and methods, see Kiibus and Kautsky (1996).

RESULTS AND DISCUSSION

Biomass

Mussels dominated the benthos, making up 96% of the biomass (Table 7.1). Their total biomass was about 114,000 tonnes (dry weight, including shells) or 43 kg per m of shoreline. There were four species of mussels whose distribution differed markedly. *C. mossambicensis* (81% of the biomass) occurred in nearly all samples, *C. africana* (9% of the biomass) was widely distributed but *Mutela dubia* (5% of the biomass) was restricted largely to shallow waters on gentle slopes with rather fine sediments. *Aspatharia wahlbergi* (5% of the biomass) was taken only at stations 15 and 18 in Basin 5 (Figure 7.1).

There were seven species of snails but they comprised only 4.1% of the biomass (Table 7.1). Their total biomass was nearly 5,000 tonnes (dry weight including shells) or 1.8 kg per metre of shoreline. *Melanoides tuberculata* (80% of the snail biomass) was widely distributed, while *Cleopatra* sp. (13% of the snail biomass) was mainly restricted to *Vallisneria aethiopica* beds and soft substrates. *Bellamya capillata* was found only in the riverine areas of Basin 1 and at the Sinamwenda River mouth (Station 7 in Basin 3). The remaining species, *Bulinus* spp., *B. pfeifferi* (Krauss) and *Lymnaea natalensis* (Krauss), were a minor part of the snail biomass (1% altogether). They were mainly found on the vegetation in rather shallow and sheltered areas. Although of low biomass, *Bulinus* spp. and *Biomphalaria pfeifferi* are important as vectors of bilharzia, a common human disease along the shores of Lake Kariba.

Some insect larvae (Chironomidae and Ephemeroptera) were probably not sampled quantitatively by the method used here. However, referring to previous studies (Machena and Kautsky 1988), we concluded that invertebrates other than molluscs constitute only a small fraction of the total animal biomass.

The vertical distribution of the fauna is shown in Figure 7.2. By collecting shells within random quadrats on exposed and dry areas of the lake shore the biomass of mussels that had existed prior to the lowering of the lake level could be estimated from the length-weight regressions given for *Aspatharia wahlbergi*, *Caelatura mossambicensis* and *Mutela dubia* by Kenmuir (1980a). From the shells collected on recently exposed bottoms we could estimate that a minimum of about 84,000 tonnes (dry weight) of mussels had been killed by stranding between 1982 and November 1984.

The mussel biomass was greatest in areas cleared of trees, the adjacent uncleared areas and some river estuaries and lowest on isolated islands and steep rocky areas.

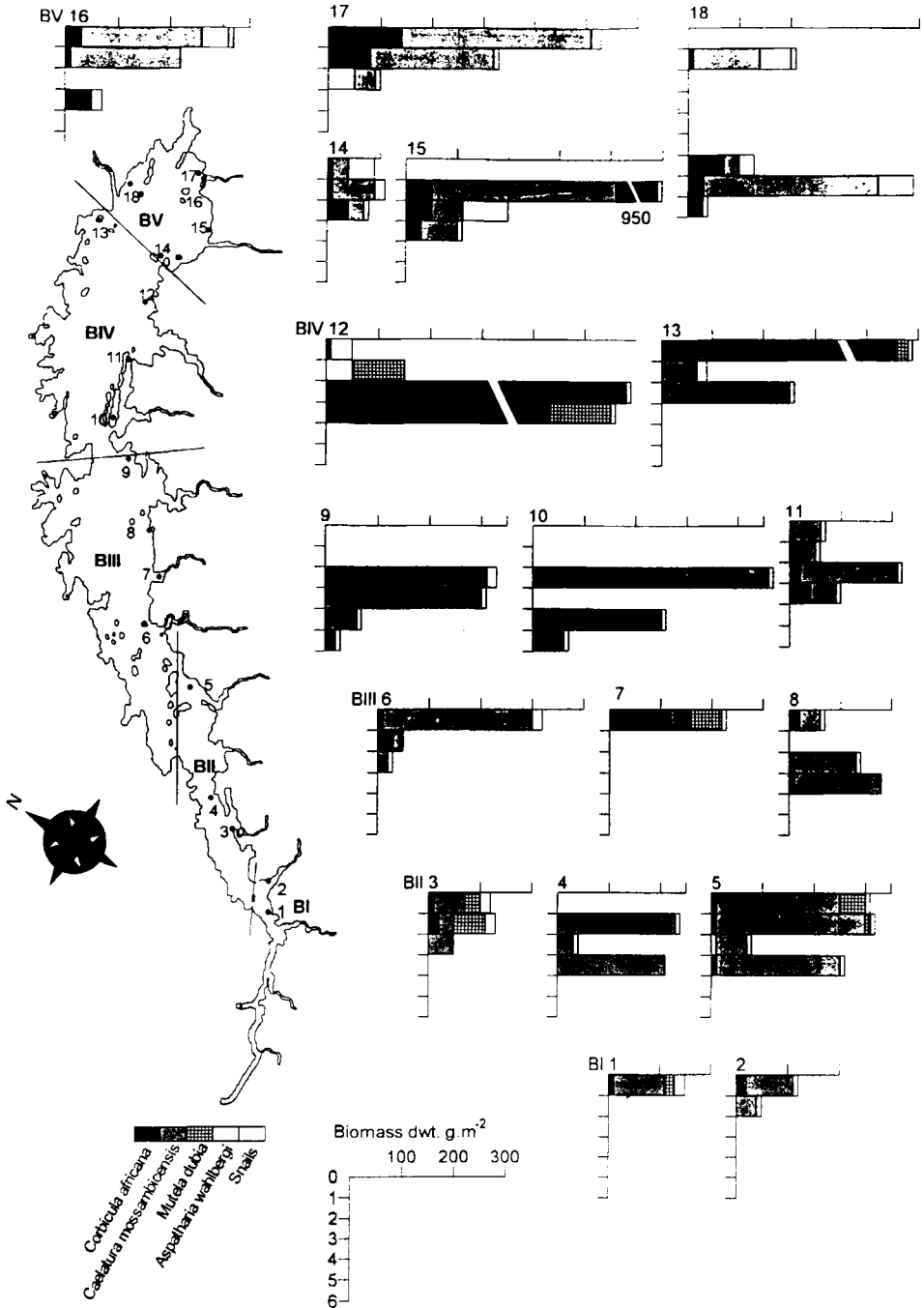


Figure 7.1 The biomass of benthic fauna (dry weight including shells) in relation to depth at different stations in Lake Kariba. Borders between major sub-basins (B1-B5), and sampling stations (1-18), are indicated (Machena and Kautsky 1988)

Table 7.1 Depth distribution of benthic fauna in lake Kariba (g m⁻² dry weight including shells) (SE of means in parentheses). Total biomasses for the lake obtained by multiplying average biomasses in each depth interval by 105.22 km² (see Machena and Kautsky 1988)

Depth interval	0-1 m (n = 40)	1-2 m (n = 27)	2-3 m (n = 14)	3-4 m (n = 16)	4-5 m (n = 3)	5-6 m (n = 3)
<i>Corbicula africana</i>	28.76 (7.58)	13.64 (3.90)	13.66 (3.84)	13.79 (3.84)	16.30 (13.40)	7.50 (7.50)
<i>Caelatura mossambicensis</i>	163.20 (31.80)	149.56 (24.33)	188.91 (50.48)	219.69 (62.81)	98.73 (55.50)	32.80 (32.80)
<i>Anatula dubia</i>	26.61 (3.82)	10.36 (4.65)	0	15.21 (7.05)	0	0
<i>Aspataria wahlbergi</i>	0	49.89 (13.8)	6.4 (6.48)	0	0	0
Total mussels	218.57	223.43	209.05	248.69	115.03	40.30
<i>Melonoides tuberculata</i>	6.781.96	5.80 (1.42)	4.47 (0.90)	5.44 (1.89)	1.57 (0.80)	5.80 (2.10)
<i>Bellamya capillata</i>	1.660.38	0.24 (0.12)	0.54 (0.15)	0.15 (0.15)	0	0
<i>Cleopatra</i> sp.	2.45 (0.58)	2.14 (0.77)	0.31 (0.13)	0.17 (0.09)	0.50 (0.50)	0.40 (0.40)
<i>Biomphalaria pfeifferi</i>	0.11 (0.03)	0.032 (0.01)	0.04 (0.03)	0.00 (0.00)	0	0
<i>Bulinus tropicus</i>	0.04 (0.02)	0.0033 (0.00)	0	0.02 (0.02)	0	0
<i>Bulinus</i> sp.	0.06 (0.01)	0.0148 (0.0)	0.04 (0.02)	0.11 (0.05)	0.01 (0.01)	0.24 (0.24)
<i>Lymnea natalensis</i>	0.02 (0.01)	0.0244 (0.01)	0	0	0	0
Total snails	11.12	8.25	5.40	5.90	2.08	6.44
Others	0	0.22 (0.05)	0.25 (0.25)	0	0	0
Total	229.69 (32.2)	231.90 (44.14)	214.7 (65.10)	254.59 (69.76)	117.11 (47.01)	46.74 (27.25)
Depth interval	6-7 m (n = 4)	7-8 m (n = 3)	9-10 m (n = 2)	Total for lake (tonnes)	Percentage in group	Total animals (%)
<i>Corbicula africana</i>	3.26 (1.04)	1.11 (1.11)	1.12 (1.12)	10431.5	9.2	8.8
<i>Caelatura mossambicensis</i>	1.92 (1.92)	20.39 (20.39)	0	92086.4	80.8	77.5
<i>Anatula dubia</i>	0	0	0	5490.4	4.8	4.6
<i>Aspataria wahlbergi</i>	0	0	0	5931.2	5.2	5.0
Total mussels	5.18	21.50	1.12	113939.6	100	95.8
<i>Melonoides tuberculata</i>	1.74 (1.45)	4.3 (4.34)	0.81 (0.81)	3866.8	79.7	3.2
<i>Bellamya capillata</i>	0	0	0	272.5	5.6	0.2
<i>Cleopatra</i> sp.	0	0	0	6.82	13.0	0.5
<i>Biomphalaria pfeifferi</i>	0	0	0	20.0	0.4	0.02
<i>Bulinus tropicus</i>	0	0	0	10.5	0.2	0.01
<i>Bulinus</i> sp.	0	0	0	50.5	1.1	0.04
<i>Lymnea natalensis</i>	0	0	0	4.2	8.6	0.003
Total snails	1.74	4.3	0.81	4925.3	100	4.1
Others	0	0	0	47.3	0.4	0.4
Total	6.92 (2.20)	15.84 (16.80)	1.93 (1.30)	118839.7		100

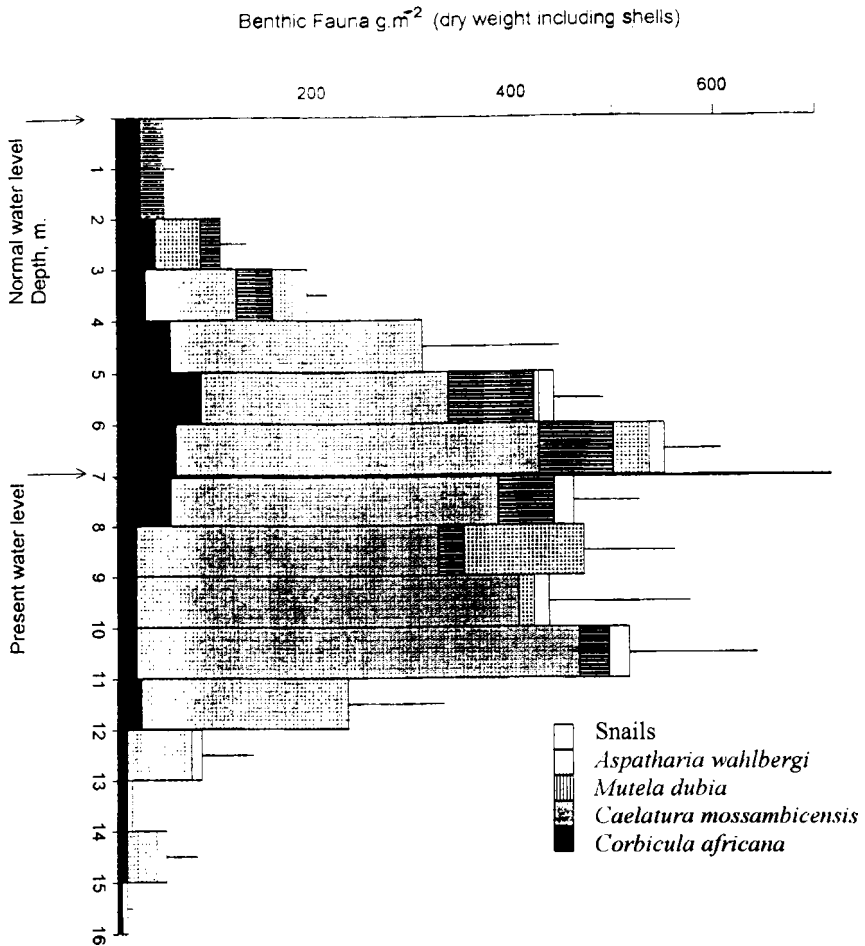


Figure 7.2 Standing stock of benthic fauna in Lake Kariba. Values below present water level were obtained by diving. Data above present water level were calculated from quantitative samples of dead shells on dry bottoms due to low water. Weights are mean dry weights including shells. S.E. of averages for all transects are given (after Machena and Kautsky 1988)

The maximum abundance of mussels was found at 3 to 9 m depth below the normal 484 m water level amounting to 190 g m^{-2} dry weight including shells. Mussel densities were lowest above about 3 m depth, i.e. at depths usually influenced by the annual water level fluctuations, and below about 7 m (the water level at the time of sampling) i.e. beyond the depths colonized by dense vegetation.

The average biomass present between 0–12 m amounted to $96.2 \pm 18.8 \text{ g m}^{-2}$ dry weight including shells ($15.0 \pm 2.9 \text{ g m}^{-2}$ shell-free dry weight). The total standing stock of mussels was estimated to be 113.940 tonnes, dry weight including shells, during the low water situation in 1984.

These findings agree with those of Kenmuir (1980a), which were obtained essentially during the 1970s. This indicates that a fairly stable situation was soon achieved after the present mussel species had colonized the lake.

Factors influencing the distribution and abundance of benthic species

The temporal and spatial distribution of benthic organisms depends on various physical and chemical factors which favour or inhibit the presence and abundance of species. Species interactions, e.g. plant-animal relationships, fish predation etc. also play an important role. Many mussels are also dependent on fish for the distribution of their larvae.

Multivariate analysis

The factors patterning the structure and distribution of the benthic vegetation and fauna in the lake have been elucidated by applying multivariate techniques to the data collected during the diving investigation (Machena 1987). Detrended canonical correspondence analyses (DCCA) (Ter Braak 1986, 1987) were run to correlate the densities of gastropods and bivalves with environmental factors and with the vegetation as explanatory variables, respectively. Three environmental variables e.g. depth, Secchi disc transparency and slope were used.

Abiotic factors

The density of four species of bivalves (*Corbicula africana*, *Caelatura mossambicensis*, *Mutela dubia* and *Aspatharia wahlbergi*) and six species of gastropods (*Melanoides tuberculata*, *Bellamyia capillata*, *Biomphalaria pfeifferi*, *Bulinus tropicus*, *Cleopatra* sp. and *Lymnaea natalensis*) are strongly correlated with slope and transparency (Figure 7.3). These two factors explain 71% of the variation in species and biomass distribution (Machena 1989). Somewhat surprisingly, the fauna showed a low correlation with depth. Except for *Caelatura mossambicensis*, all the bivalve and gastropod species prefer gentle slopes and low transparency. Low transparency implies a turbid environment which could provide suspended organic matter as feed for the filter feeders.

McLachlan (1969, 1974, 1979) and Petr (1970a, b) have detailed some of the factors controlling colonization of new substrata, particularly in fluctuating endorheic systems (Chilwa) and man-made lakes (Lakes Kariba and Volta). Considerable shoreline vegetation is drowned as water rises, allowing rapid colonization by active migration of Chironomidae (McLachlan 1969), Trichoptera, Chironomidae, Oligochaeta and Ephemeroptera (Petr 1970a).

These "pioneer" groups rapidly increase in density and biomass, but their populations can crash with equal rapidity as substratum losses occur.

Burgis *et al.* (1973) and Darlington (1976) have shown that the texture and stability of the substrate of Lake George is primarily responsible for variations in horizontal distribution of benthos (possibly accounting for 30–40% of the total variation between samples (Darlington 1976). Comparable influences exist in Lake Chad (Lévêque 1979), where depth-related wind-induced turbulence and resuspension of unstable bottom sediments lead to "blanketing" effects on the fauna (Dejoux 1976) and limit the depth penetration of molluscs (James 1985). Furthermore, depth limitation may be enhanced by food stress, due to low plankton densities and decreased water exchange below the thermocline.

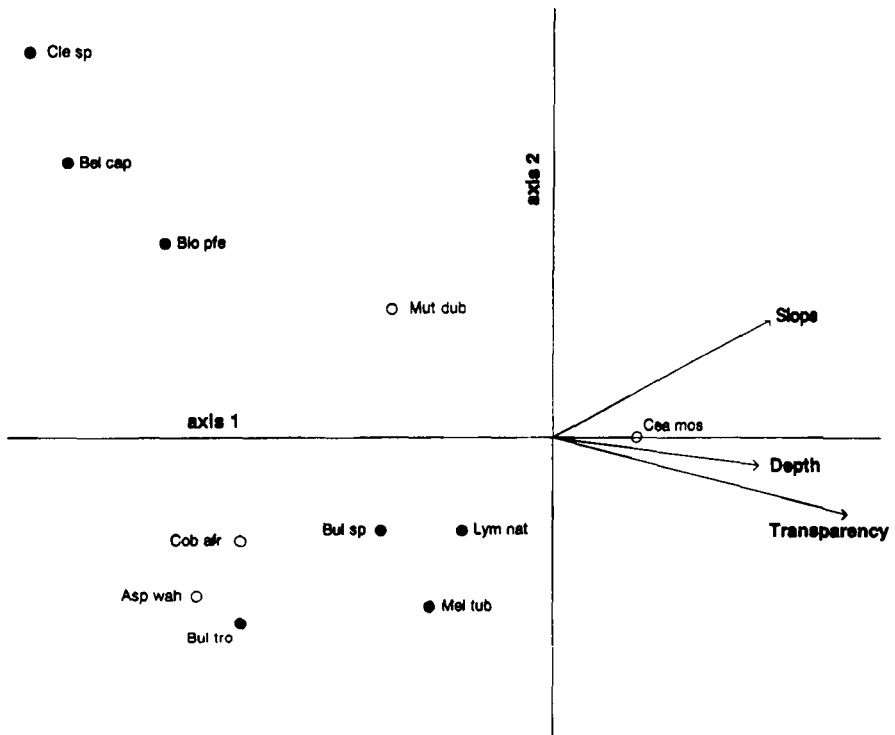


Figure 7.3 Ordination diagram based on canonical correspondence analysis of gastropods (●) and bivalves (○) with respect to three environmental variables: depth, slope and transparency (shown by arrows). Cor afr = *Corbicula africana*; Cae mos = *Caelatura mossambicensis*; Mut dub = *Mutela dubia*; Asp wah = *Aspataria wahlbergi*; Mel tub = *Melanoides tuberculata*; Cle sp = *Cleopatra sp.*; Bel cap = *Bellamyia capillata*; Bio pfe = *Biomphalaria pfeifferi*; Bul tro = *Bulinus tropicus*; Bul sp = *Bulinus sp.*; Lym nat = *Lymnea natalensis*

The depth range of species is also modified by factors that are not exclusively depth controlled, such as bottom type, slope and wave exposure. However, these factors may affect turbulence, sediment particle size, turbidity etc. (Segal 1971, Briston *et al.* 1977).

In man made lakes, the strong influence of draw-downs on the performance of the littoral flora and fauna can be seen in the Cahoon Bassa reservoir situated further down the Zambezi River where annual draw-downs of between 6 and 14 m completely prevent the establishment of submerged macrophytes (Bernacsek and Lopes 1984), and probably also restricts mussel distribution severely. More generally, water level fluctuations have large impacts on the littoral fauna which may become dried out when the water levels are going down. If these fluctuations are too quick and too large, colonization by long-lived species may also be hindered.

Low oxygen may restrict the development of fauna at depths below the thermocline. This was probably more acute during the early more eutrophic stages

of the lake, especially in areas covered by *Salvinia* mats. However, this may be an important factor as benthic fauna seems to be scarce below the thermocline. Temperature limitation is not likely in Lake Kariba since the minimum temperature of the bottom water is always above 20°C (Balon and Coche 1974).

Benthos vegetation interaction

It is apparent that at least one bivalve and four gastropods are also related to macrophyte distribution. The distribution of *Caelatura mossambicensis* is related to that of both *Lagarosiphon ilicifolius* and *Najas pectinata*. That of the gastropods *Bellamyia capillata*, *Biomphalaria pfeifferi*, *Bulinus tropicus*, *Cleopatra* sp. and *Lymnaea natalensis* is related to *Vallisneria aethiopica* and *Potamogeton octandrus* (Figure 7.4).

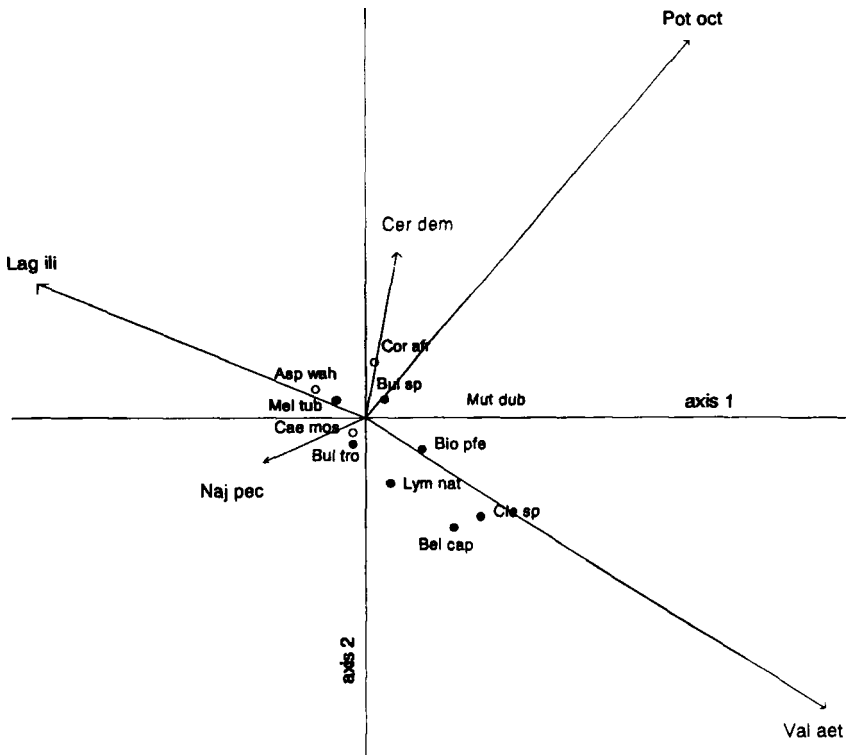


Figure 7.4. Ordination diagram based on canonical correspondence analysis of gastropods (●) and bivalves (○) with respect to five environmental variables (vegetation species shown by arrows). Lag ili = *Lagarosiphon ilicifolius*; Naj pec = *Najas pectinata*; Cer dem = *Ceratophyllum demersum*; Pot oct = *Potamogeton octandrus*; Val aet = *Vallisneria aethiopica*; Cor afr = *Corbicula africana*; Cae mos = *Caelatura mossambicensis*; Mut dub = *Mutela dubia*; Asp wah = *Aspataria wahlbergi*; Mel tub = *Melanoides tuberculata*; Cle sp = *Cleopatra* sp.; Bel cap = *Bellamyia capillata*; Bio pfe = *Biomphalaria pfeifferi*; Bul tro = *Bulinus tropicus*; Bul sp = *Bulinus* sp.; Lym nat = *Lymnaea natalensis*

The importance of vegetation for the biomass of benthos was also observed in Swartvlei Lake (Davies 1979), where the increased surface area provided by dense stands of *Potamogeton pectinatus* resulted in standing stocks of benthos that were four orders of magnitude greater than those supported by sand-mud substrata. How far this increase reflects increased food availability and shelter from predators, or merely reflects increased number or area of sites for colonization, is not known.

Gastropod-vegetation interaction

There is a strong correlation between the abundance of gastropods and the vegetation, possibly because of variations in the abundance and composition of epiphytes on different plant species, abundance and structure of the vegetation itself (Machena 1989). The gastropods either feed directly on the vegetation or graze on the epiphytes and detritus.

In agreement with the observations of S. Björk-Ramberg (pers. comm.), it appeared that *V. aethiopica* had a lower biomass of epiphytes than *L. ilicifolius* and *N. pectinata* because of heavier grazing on *V. aethiopica*. The most common gastropod in Lake Kariba, *Melanoides tuberculata*, is, however, not associated with vegetation but prefers other habitats i.e. sediment bottoms since it is a detritus feeder.

Carpenter and Lodge (1986) suggest that grazers could be chemo-attracted to macrophytes, and Brönmark (1985) found that *Lymnaea peregra* was attracted to chemicals excreted by *Ceratophyllum demersum*. According to Welch (1952), *Vallisneria americana* has a high protein and carbohydrate content which makes it more palatable than other species. This could apply to *V. aethiopica* but it is equally possible that in Lake Kariba *V. aethiopica* and *Potamogeton octandrus* are more palatable than e.g. *Lagarosiphon ilicifolius* and *Najas pectinata* for the same reason. Furthermore, the wider leaves of *Vallisneria* and *Potamogeton* provide a better climbing surface than the leaves of *Ceratophyllum demersum*, *N. pectinata* and *L. ilicifolius* which are highly dissected and tiny and might not be suitable for snail climbing (Lodge 1985). In Lake Malawi, Brown (1978) also reported that *Bulinus succinoides* is found largely on *V. aethiopica*.

Brönmark (1985) also observed that grazing on *C. demersum* actually enhanced the growth rate of the plant. Similarly, Cattaneo and Kalff (1980) also found that *Myriophyllum spicatum* and *Elodea canadensis* with highly dissected leaves had a denser growth of epiphytic algae than the broader-leaved *V. americana* and *Potamogeton richardsonii*.

These are indications of mutual relationships between grazers and macrophytes.

Mussel-vegetation-correlations

Caelatura mossambicensis was found to be associated with *Lagarosiphon ilicifolius* and *Najas pectinata*, the dominant plant species, although it does not feed directly on the vegetation. Instead, bivalves are filter feeders and phytoplankton and suspended organic matter like detritus with associated microbial flora comprise their food. The bivalve association with vegetation could be either direct or indirect, through coinciding habitat requirements. In the former situation, vegetation stands could provide a suitable sheltered and nutrient-rich environment as *L. ilicifolius* communities have a very high productivity which

ensures a high turnover rate of detrital matter (Machena *et al.* 1990). In the latter situation, bivalves prefer gently sloping areas with reduced wave activity and a lower risk from wave-induced sediment material (Kenmuir 1980a) which are also areas with high biomass of vegetation (Machena 1987).

Mussel-fish correlations

Both the vertical and horizontal distributions of mussels that have parasitic glochidia larvae (i.e. all species in the lake except *Corbicula africana*), are likely to be influenced by the distribution of the fish hosts (Kenmuir 1980a, Strayer *et al.* 1981). For example, Kenmuir (1980a) found *Caelatura mossambicensis* aggregated at the bases of objects, such as rocks and tree trunks or underneath fallen branches or bark, which he attributed to the fact that this is the habitat of dwarf bream, *Pharyngochromis darlingi* (Boulenger), which may be the host species of glochidia of *Caelatura*. In the same way, *Mutela dubia* was often found aggregated around tree trunks and *Aspatharia wahlbergi* was found mainly in riverine areas (Begg 1970). Similarly, fish associated with vegetation would probably seed mussels in such habitats.

Mussel-bird correlations

When the lake level is low and mussels are found in shallow water or even exposed on dried out shores they may be taken by terrestrial predators and scavengers. A conspicuous species that can be found in large numbers on the lake during periods of low water are African openbilled storks, *Anastomus lamelligerus*, a specialised mussel predator that is largely dependant on the availability of *Mutela dubia* in the lake (Eriksson and Kautsky 1992). Although the occurrence of the mussel seems important for this avian predator, the impact of the predation on the mussel population is most likely small. This is verified by the fact that most of the stranded mussels die from desiccation during periods of falling water level (see also Hustler this volume).

Benthic biomass compared to other lakes

The biomass found today in Lake Kariba is very high when compared with the situation in the lake before the mussels established, when McLachlan (1967) and McLachlan and McLachlan (1971) estimated the biomass to be in the range 0.1–0.3 g m⁻², mainly made up of chironomids. During periods of stable water levels, maximum biomass then occurred at about 2 m depth (23 species, 0.5 g dry weight m⁻²), with the fauna disappearing at water depths of 8 to 12 m.

Remarkably lower numbers of insects and insect larvae were found in Lake Kariba during the 1984 survey (Machena and Kautsky 1988), and it has been speculated that this might have been due to the increased use of insecticides in the area (Berg *et al.* 1992), although the evolution of the fish fauna and the establishment of other insect predators since the 1960's might also have contributed to the reduction in insects.

The biomass found today (96.2 g m⁻², dry weight including shells in the first meters) is also very high compared to other tropical lakes. For the very shallow Lake Chad (mean depth 4 m.), Lévêque *et al.* (1983) give a mean benthic biomass of 3.7 g m⁻² of which 3.3 g m⁻² was due to molluscs, 0.29 g to oligochaetes and 0.12 g to chironomids. Contrary to the situation in Lake Kariba, snails dominate that lake, contributing 83% of the mollusc biomass. The benthic biomass of Lake

McIlwaine (Zimbabwe), a reservoir with a mean depth of 10 m (31 m maximum) can be estimated at about 3 g m^{-2} from the data of Munro (1966), while Marshall (1978) estimated standing crops of between 2.6 and 15.2 g m^{-2} , mainly oligochaetes and chironomids in the 0–20 m depth interval of the lake. Biomass values from some other African lakes amount to 3.0 g m^{-2} for Lake Chilwa (McLachlan 1979), 0.98 to 1.13 g m^{-2} (mainly insect larvae) for Lake George (Darlington 1976) and 0.01 to 3.26 g m^{-2} for Lake St. Lucia (Bolt 1975). Moreover, in the brackish Swartvlei, also dominated by mussels, the biomass is 9.08 to 141.36 g m^{-2} (Davies 1979), comparable to what found in shallow littoral waters of Lake Kariba. In Muchison Bay in Lake Victoria, the total benthic biomass was as high as 730 g m^{-2} (wet weight) (Okedi 1990).

For at least some of these lakes, the biomass may be underestimated, because the sampling methods used may not have been appropriate for quantifying molluscs. In particular, abundant bivalve and pulmonate shells could be seen on the shore during extreme low water periods in both Lake Chilwa and Lake McIlwaine (Marshall 1975). Furthermore, several of these lakes show large seasonal variations in biomass mainly due to water level fluctuations (e.g. Lake Chad, Lake Chilwa, Lake McIlwaine) or salinity variations (e.g. Lake St. Lucia and Swartvlei).

The large mussel biomass (114,000 tonnes) found in Lake Kariba is probably due to the extremely low degree of predation on adult mussels, as there is no efficient fish predator on adult mussels in the lake. In the ancient Lake Tanganyika, e.g. this niche is occupied by the catfish, *Synodontis multipunctatus*, which feeds almost exclusively on mussels (Brichard 1978). With little predation the main mortality factor in Lake Kariba would be natural death from age (Kautsky 1981), excessive sedimentation, or drying out during extreme low water. Because recruitment seems to be density-dependent (Kenmuir 1980a), we can infer that the mussel population is at its carrying capacity with regard to available habitat and food. The introduction of, or natural colonization by, a mussel-eating fish might change these conditions completely, and would probably result in a lowering of the total benthic invertebrate biomass.

Small scale attempts to exploit the mussels for human food were made during the times of receding water levels in the early 1980's. The mussels were smoked or canned and sold to hotels etc., but local populations did not prove very keen on including them in their diet. In addition, the business was discontinued possibly due to decreased mussel availability when the water level rose again. In theory, the Kariba mussels could also be utilized as human food indirectly through the introduction of a mussel predator like *Synodontis multipunctatus*, which could then be harvested. Careful studies on the impact of the fish in the new environment need, however, to be carried out before any introduction is considered, since exotic fish species are likely to compete with native species if they have similar niche requirements, particularly food and habitat, which may lead to the extinction of native species.

As already mentioned, the biomass of macrophytes, mussels and snails in 1984 was clearly influenced by the past three years drought, that resulted in a substantial lowering of water level of 7 m. After a few years of normal annual draw-downs of about 3 m, we estimate that the average macrophyte and mussel biomass might increase to about 100 and 150 g m^{-2} , respectively, for the 0–12 m

interval (Machena and Kautsky 1988). Snails may not respond to the same extent because of their higher turnover rate, with generally several generations per year.

Production of benthos

The production of benthos can be roughly calculated by using estimates of production over biomass (P/B) ratios obtained for the populations under consideration, or similar ones (Winberg *et al.* 1971, Zaika 1973). Kenmuir (1980a) established such ratios for *Caelatura mossambicensis*, *Aspatharia wahlbergi* and *Mutela dubia* in Lake Kariba. Data for *Corbicula africana* and for the major snail species were obtained from Lake Chad (Lévêque and Saint-Jean 1983). Combining these P/B ratios with our biomass data, we have calculated the production of the main benthic invertebrate species for the total lake as well as for the littoral zone between 0–12 m depth (Table 7.2).

Table 7.2 Production of benthic animals in lake Kariba and the littoral zone. P/B ratios from:

- 1) Lévêque *et al.* (1977), Lévêque and Saint Jean (1983),
- 2) Kenmuir (1980a),
- 3) estimated.

Conversion to organic drywt. for mussels from Kenmuir (1980b), and for snails from Lévêque *et al.* (1983). For conversion from total biomasses for the whole lake to m^{-2} see Table 7.1

Species	Total biomass (tonnes)	P/B -ratio (annual)	Production (tonnes yr^{-1})	Littoral production ($\text{g m}^{-2} \text{yr}^{-1}$) org. dry wt.
<i>Corbicula africana</i>	10431	2.60 ¹⁾	27121	3.33
<i>Caelatura</i> <i>mossambicensis</i>	92086	0.44 ²⁾	40518	4.97
<i>Mutela dubia</i>	5490	0.44 ²⁾	2416	0.30
<i>Aspatharia wahlbergi</i>	5931	0.29 ²⁾	1720	0.21
Total mussels	113940		71775	8.81
<i>Melonoides</i> <i>tuberculata</i>	3867	4.40 ¹⁾	17014	1.63
<i>Bellamyia capillata</i>	272	5.80 ¹⁾	1580	0.18
<i>Cleopatra</i> sp.	628	2.60 ¹⁾	1633	0.29
<i>Biomphalaria</i> <i>pfeifferi</i>	20	5.00 ³⁾	100	0.01
<i>Bulinus</i> sp.	60	5.00 ³⁾	304	0.04
<i>Lymnea natalensis</i>	4	5.00 ³⁾	21	0.01
Total snails	4925		20652	2.16
Others	47	5.00 ³⁾	236	0.03
Total fauna	118840		92663	11.00

The average production of benthic animals in the populated littoral zone (0–7 m depth when sampling) amounted to $11.0 \text{ g m}^{-2} \text{yr}^{-1}$ (org. dry weight) of which the slower growing mussels accounted for 8.81 g and the more highly productive snails contributed 2.16 g, while insects made up only 0.03 g. The most important individual species in the lake are *Caelatura mossambicensis* ($4.97 \text{ g m}^{-2} \text{yr}^{-1}$), *Corbicula africana* (3.33 g) and *Melanoides tuberculata* (1.63 g).

Benthic production in other tropical lakes

Production estimates for benthic invertebrates from other tropical lakes are relatively scarce. For the shallow Lake Chad with a biomass of 3.7 g m^{-2} , production has been estimated at $18 \text{ g m}^{-2} \text{ yr}^{-1}$ (Carmouze *et al.* 1983). The corresponding values for the shallow waters of Lake Kariba are an average biomass of 3.43 g m^{-2} and an average annual shell-free production of $11 \text{ g m}^{-2} \text{ yr}^{-1}$. The higher production values in Lake Chad are probably mainly due to the fact that snails, oligochaetes and insect larvae with high production rates dominate whereas more slowly growing mussels are predominant in Lake Kariba. In Lake Nakuru, the benthic biomass is only 0.43 g m^{-2} , but since it is dominated by chironomids the daily production rates are on an average $40.1 \text{ mg dry wt m}^{-2}$ (Vareschi and Jacobs 1984), corresponding to about $14.6 \text{ g m}^{-2} \text{ yr}^{-1}$.

Respiration, nutrient excretion and water filtration in mussels

Few studies have been made on the metabolism of tropical species at high temperatures, although bioenergetic analysis holds a potential key to understanding functional responses of aquatic invertebrates (Griffiths and King 1979 a and b, Hart 1980 a and b, Clarke and Griffiths 1990, Cookcroft 1990).

Kiibus and Kautsky (1996) have measured how the size of the mussels and the water temperature affects the metabolism in laboratory experiments. Respiration and the excretion of nutrients ($\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$) was assessed for different sizes of freshly collected mussels (*Aspatharia wahlbergi*, *Corbicula africana* and *Caelatura mossambicensis*) at 25.2°C and for *A. wahlbergi* and *C. africana* some of these parameters were also measured at higher and lower temperatures. The variation with size in the filtration (clearance) rate of *Aspatharia wahlbergii* was also assessed.

As expected, the weight specific rates of respiration, nutrient excretion and filtration all decrease with size in the mussels (Figures 7.5 and 7.6). Thus, the smallest species, *Corbicula africana*, also has a much higher individual rate than the other species. The equations are given in Table 7.3.

Table 7.3 Equations of weight-specific metabolic relationships in Lake Kariba mussels. The correlation coefficient R is also given. x is given in g dry weight. The data are plotted in Figures 7.5 and 7.6 (from Kiibus and Kautsky 1996)

Respiration ($\text{mg O}_2 \text{ g}^{-1} \text{ h}^{-1}$)			
• <i>Aspatharia wahlbergi</i>	$y = 0.765 x e^{-0.252 x}$	$R = 0.91$	$n = 19$
• <i>Caelatura mossambicensis</i>	$y = 0.765 x e^{-0.159x}$	$R = 0.53$	$n = 8$
$\text{NH}_4\text{-N}$ excretion ($\mu\text{g NH}_4\text{-N g}^{-1} \text{ h}^{-1}$)			
• <i>Aspatharia wahlbergi</i>	$y = 0.765 x e^{-0.320x}$	$R = 0.95$	$n = 19$
• <i>Caelatura mossambicensis</i>	$y = 0.765 x e^{-0.127x}$	$R = 0.36$	$n = 8$
$\text{PO}_4\text{-N}$ excretion ($\mu\text{g PO}_4\text{-P g}^{-1} \text{ h}^{-1}$)			
• <i>Aspatharia wahlbergi</i>	$y = 0.765 x e^{-0.333x}$	$R = 0.93$	$n = 19$
• <i>Caelatura mossambicensis</i>	$y = 0.765 x e^{-0.313x}$	$R = 0.68$	$n = 8$
Filtration rate ($\text{l g}^{-1} \text{ h}^{-1}$)			
• <i>Aspatharia wahlbergi</i>	$y = 0.765 x e^{-0.188x}$	$R = 0.81$	$n = 10$

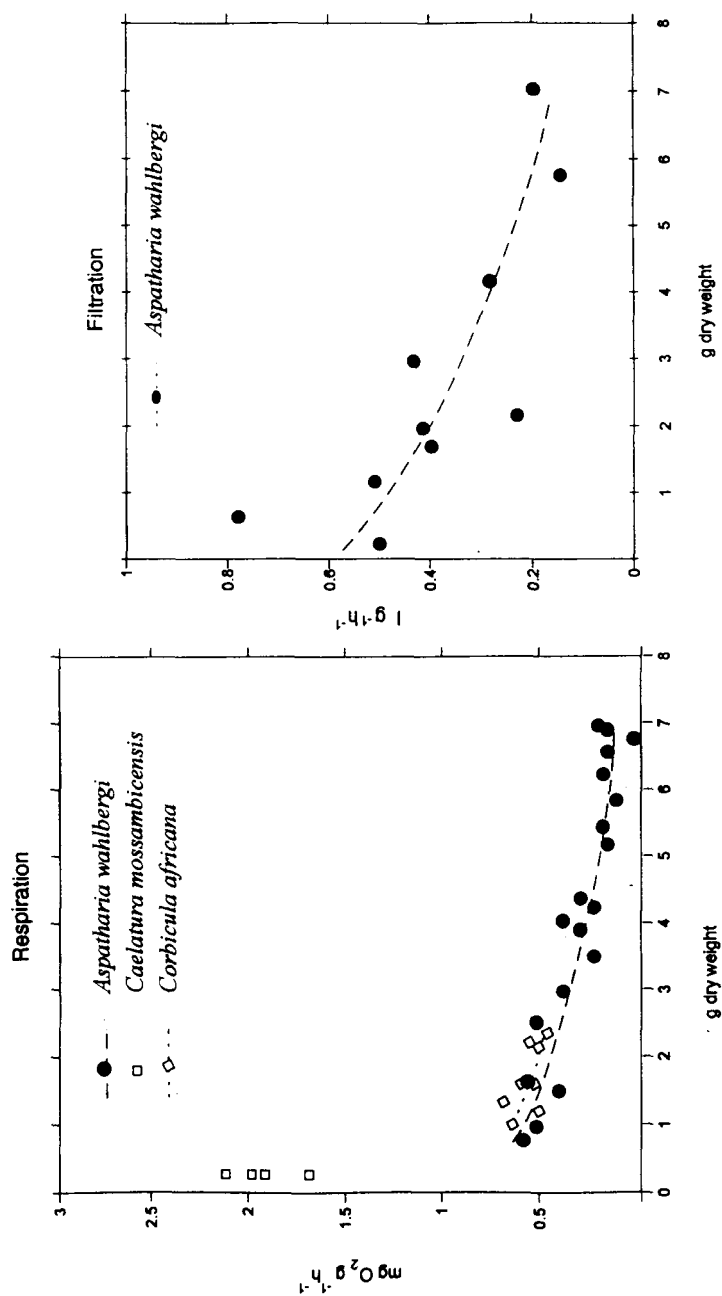


Figure 7.5 Respiration (left) and filtration (right) rate in mussels of different sizes from Lake Kariba measured in the laboratory at 25.2°C (data from Kiibus & Kautsky 1996)

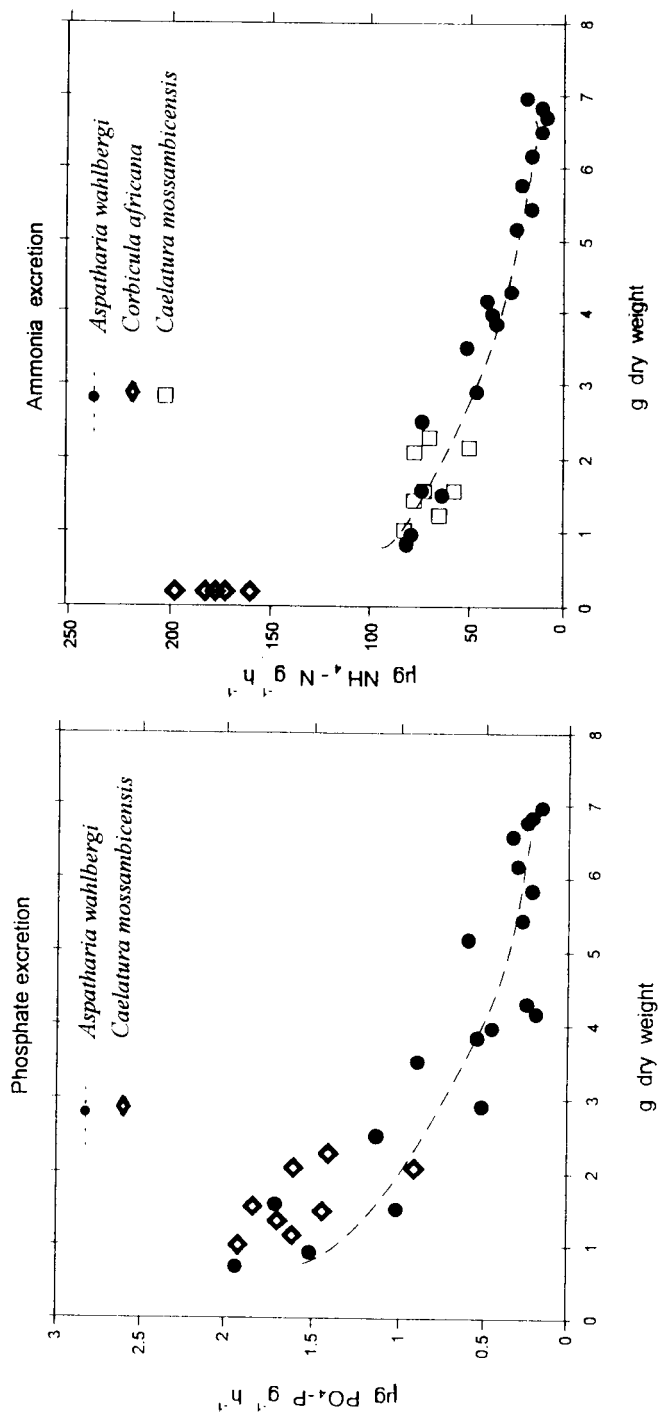


Figure 7.6 Phosphate (left) and ammonia (right) excretion in mussels of different sizes from Lake Kariba measured in the laboratory at 25.2°C (data from Kiibus & Kautsky 1996)

This activity was found to vary also with temperature, displaying a bell-shaped relationship (Figure 7.7). Metabolism in *Aspatharia wahlbergi* increased with temperature from 16.5°C reaching a maximum at 34°C and then decreased again. At 16.5°C activity was slow but continuous and the water was clear with little production of mucus. At 23.2°C and 25.2°C activity seemed to be normal with some production of mucus, while at 29.3°C and 34°C the activity was increased with fairly high mucus production. The mussels also showed signs of stress at 34°C moving around in the containers once or twice during the experiment. There were also shorter periods of inactivity when they closed their shells at this temperature. At 39°C, the mussels were severely stressed alternating between active periods when they were "coughing" and moving around and longer periods of total closure and inactivity. Mucus production was very high and the water soon became turbid at this temperature.

The pattern of *Corbicula africana* was rather similar, although the metabolism was fairly constant between 18.6 and 29.2°C, implying a quite broad temperature tolerance. However, above 29.2°C respiration decreased markedly, indicating a lower tolerance to extremely high temperatures than *Aspatharia*.

Excretion of $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ in *Aspatharia* showed a similar pattern with about five times increase in rates between 16.5 and 34.0°C, which was followed by a decrease at 39.0°C.

The average respiration, excretion and filtration rates per $\text{h}^{-1} \text{g}^{-1}$ for an average sized 1g mussel (shell-free dry weight) at 25.2°C are estimated to about 0.6 mg O_2 , 85 μg $\text{NH}_4\text{-N}$, 1.5 μg $\text{PO}_4\text{-P}$ and 0.5 l water filtered (Figure 7.5 and 7.6).

Similar measurements are scarce for tropical areas (Rodriguez-Ortega 1978, McMahon 1979, Foe and Knight 1986) but the results found here are comparable to those given for related species from temperate areas (Stancykowska *et al.* 1976), although the temperature optimum seems to be higher in Lake Kariba. As expected, the tolerance to high temperatures is also much higher in Lake Kariba species that are used to naturally occurring high temperatures. In very shallow densely vegetated bays maximum temperatures as high as 45°C have been observed, which indicates that temperatures in nature may reach levels that kill mussels. Kenmuir (1980a) reports that temperatures in marginal shallow water may increase by 25–30°C during a day in marginal shallow water and that *Caelatura mossambicensis* was able to withstand a water temperature of 42.2°C for a short period, but that a state of dysfunction was manifested at a temperature of 41.5°C. In another experiment *Aspatharia wahlbergi* survived 3 months if put dry on a tray in the laboratory at 21–30°C and started to pump water again after being put in water, while *Caelatura mossambicensis* and *Mutela dubia* died within 6 days. *A. wahlbergi* seems to be better adapted to live in water bodies that dry out also as it generally digs into the sediment while the other species remain at the surface when they become exposed to air (Kenmuir 1980a).

CONCLUSION: IMPACT AND ROLE OF MUSSELS

Mussels in Lake Kariba represent a biomass resource that is presently not being fully exploited by other organisms.

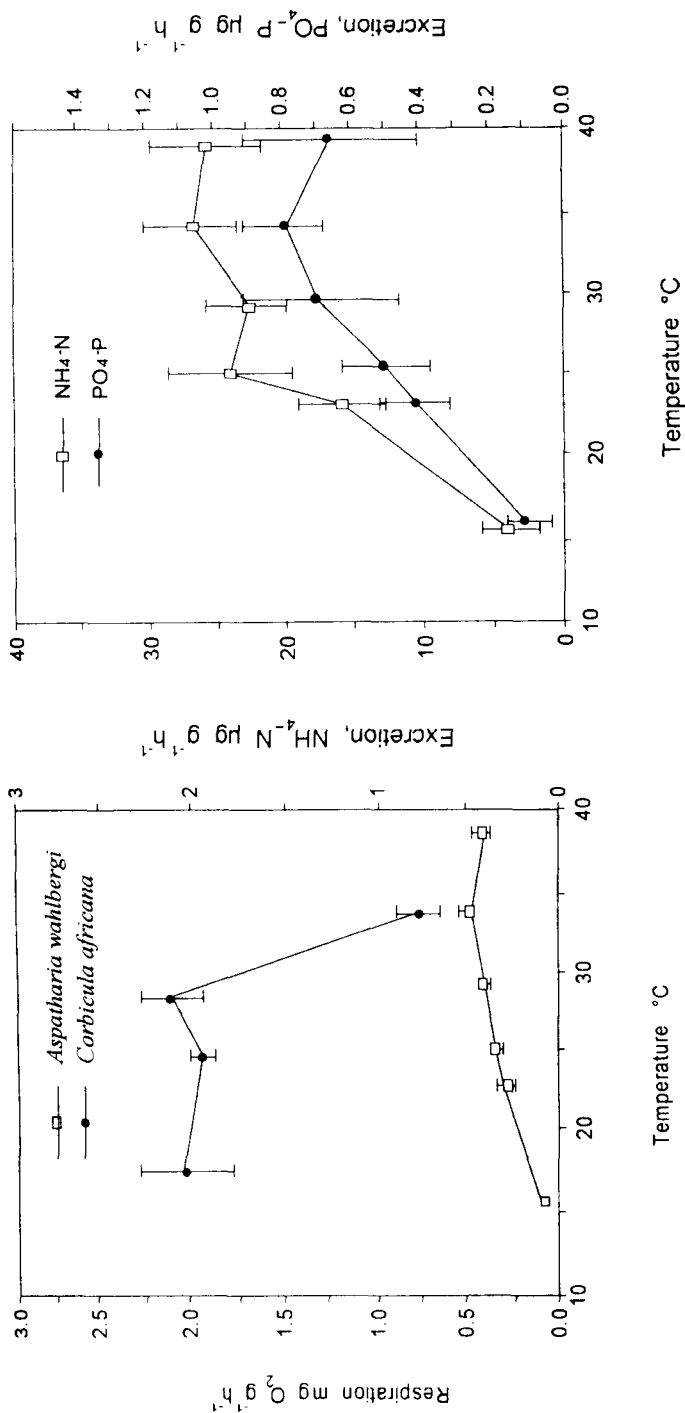


Figure 7.7 Left: changes in respiration with temperature of mussels (*Aspatharia wahlbergi*, *Corbicula africana*) from Lake Kariba (data from Kibus and Kautsky 1996)
Right: changes in nutrient excretion ($\text{PO}_4\text{-P}$ and $\text{NH}_4\text{-N}$) with temperature of *Aspatharia wahlbergi* from Lake Kariba (data from Kibus and Kautsky 1996)

A similar situation exists in Lake Victoria, where the rich benthic fauna is under-utilized by organisms at higher trophic levels and hence represents utilizable organic matter for man (Okedi 1990).

Although one third of the diet of the cichlids consists of mussels (Machena *et al.* 1993), predation seems to have little effect on the mussel population.

However, it should be noticed that, to some extent, the mussels may compete with fish for food, since the primary production of the pelagic system constitutes the common food base for both mussels and kapenta *Limnothrissa miodon*. While mussels take their food directly at the primary producer (or detritus) level, in the restricted littoral zone of the lake, kapenta essentially feeds at a step higher in the food chain (the zooplankton level), which further increases the food-base needed for sustaining the fish stock.

Filtering organic particles from the water and remineralizing and recirculating nutrients back to the primary producers may be the most important ecological function of mussels in the lake. Kiibus and Kautsky (1996) estimated the magnitude of such an impact by multiplying the average metabolic rates (Figures 7.5 and 7.6, Table 7.3) by the biomass of mussels (17,784 tonnes shell-free dry weight), which gave a volume corresponding to the total epilimnion of the lake (i.e. $7.9 \times 10^{10} \text{ m}^3$) that is filtered by the mussel population every year, and that 13,000 tonnes total inorganic nitrogen and 230 tonnes of inorganic phosphorus are remineralized annually by the mussel population. Furthermore, the population consumes 9.3×10^4 tonnes oxygen per year indicating that the population needs 3.5×10^4 tonnes of organic carbon for its maintenance, which means that a substantial amount, of the primary production is channelled through mussels. Still, these values should rather be regarded as minimum estimates since *in situ* measurements of mussel metabolism may give up to two times higher rates (Kautsky and Wallentinus 1980).

The role of mussels in cycling nutrients in Lake Kariba can be evaluated by comparing rate measurements to total loading from outside sources. While the total mean load of phosphorous into the lake is about 1,025 tonnes per year (Magadza *et al.* 1989), mussels remineralize 230 tonnes of phosphorous or about 1/4 of the total load over the same period. For nitrogen, the total load into Lake Kariba is 1684 tonnes yr^{-1} , whereas mussels remineralize as much as 13,000 tonnes yr^{-1} , or 8 times the annual inputs. These comparisons are however uncertain since Magadza *et al.* (1989) largely based their estimates on rather incomplete data from Balon and Coche (1974). Probably the inputs are underestimated. Literature data show that in temperate areas phosphate turnover may occur approximately 20 times a year (Golterman 1975) whilst in the Lago Januauaca and several East African lakes it can occur as frequently as every 1–3 hours (Peters and MacIntyre 1976, Fisher and Parsley 1979). These data include also the remineralization by microbial organisms, zooplankton and other organisms. In Lake George the phytoplankton feeders (copepods and two cichlid fish species) recycled rather more nitrogen within the lake than entered it in a year and, with regard to phosphate, they proved to recycle two to three times the annual input (Ganf and Viner 1973). Few studies have focused on mussels in this respect. In Lake St. Clair the mussel population filtered about 13.5% (210 tonnes out of 3,100 tonnes totally) of the total phosphorous load. Of this amount about 134 tonnes was sedimented to the bottom via biodeposition. (Nalepa *et al.* 1991).

Mussels may therefore contribute significantly to nutrient cycling in Lake Kariba, especially with regard to nitrogen. It should be remembered that these are data for the total lake, whereas turnover rates in the littoral areas where the mussels are concentrated are certainly much higher indicating that mussels are probably of even greater significance for the flows of energy and matter within these areas.

It is well known from other areas that mussels can play an important role in the nutrient dynamics of water bodies (Kuenzler 1961, Lewandowski and Stanczykowska 1975, Walz 1978, Kautsky and Wallentinus 1980, Dame *et al.* 1980, Kautsky 1981b, Stanczykowska and Planter 1985, James 1987, Kautsky and Evans 1987). As filter-feeders, they circulate and regenerate large amounts of nutrients, which are immediately available for new primary production as they are excreted in the surface water of the lake (Kautsky and Wallentinus 1980). Thus, the mussels speed up remineralization and regenerate nutrients in the photic zone, compared to the situation in offshore areas where dying plankton may largely sediment to the hypolimnion (Kautsky 1981b, Kautsky and Evans 1987, Nalepa *et al.* 1991). This material is remineralized at a slower rate in the bottom sediments and will be returned to the trophogenic layer only after turnover. Mussels in Lake Kariba thus act as a connecting link between the benthic and pelagic system.

Furthermore, in Lake Kariba and other reservoirs with turbine intakes situated below the thermocline, some of the nutrients remineralized in the deep water will never return to the surface layers but will be drained through the outflow (Begg 1970). With the development of the littoral communities in Lake Kariba we can infer that this drainage has been lowered substantially.

Regular and unpredicted variations in the water level will, as mentioned earlier, have large effects on the biomass of littoral communities, which will naturally also have effects on the impact of mussels on the functioning of the total lake ecosystem.

SUMMARY

The distribution and biomass of the benthic fauna, surveyed in Lake Kariba in November 1984, was found to be similar to that of the vegetation. The total animal biomass of 118,840 tonnes dry weight, including shells, consisted of mussels (95.8%), snails (4.1%) and insect larvae (0.1%). Four species of mussels were found: *Caelatura mossambicensis* (von Martens) (81% of mussel biomass), *Corbicula africana* (Krauss) (9%), *Mutela dubia* (Gmelin) (5%) and *Aspatharia wahlbergi* (Krauss) (5%). The most abundant snails were *Melanoides tuberculata* (Müller), *Cleopatra* sp. and *Bellamya capillata* (Frauenfeld).

The biomass was high compared to that recorded in most other lakes, probably due to a lack of predators. For the colonizable 0–12 m depth interval and the total lake it was 96.2 g m⁻² including shells (15.0 g m⁻² shell-free dry weight) and 22.6 g m⁻² including shells (3.4 g m⁻² shell-free dry weight), respectively. The annual production of benthos for the 0–12 m interval was estimated at 11.0 g m⁻² yr⁻¹ (shell-free dry weight), and for the total lake it was 2.70 g m⁻² yr⁻¹ (shell-free dry weight).

A multivariate direct gradient analysis showed that the abundance of various species found in Lake Kariba were correlated with environmental variables such as slope and transparency of the water. A stepwise regression analysis further

showed interdependence between the gastropods *Cleopatra* sp., *Biomphalaria pfeifferi*, *Lymnea natalensis*, *Bellamya capillata* and the macrophyte *Vallisneria aethiopica* on one hand and between the mussel *Caelatura mossambicensis* and the macrophytes *Lagarosiphon ilicifolius* and *Najas pectinata* on the other hand.

The average respiration, nutrient excretion and water filtration rates for mussels in Lake Kariba at 25.2°C were estimated to about 0.6 mg O₂, 85 µg NH₄-N, 1.5 µg PO₄-P and 0.5 l water filtered h⁻¹ g⁻¹ shell-free dry weight. This gives that a volume corresponding to the total epilimnion of the lake is filtered by the mussels annually. We conclude that the mussels, rather than being an important food source for fish, seem to play a very large role in the nutrient dynamics of Lake Kariba.



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